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THE LIKELIHOOD OF PERSISTENCE OF SMALL POPULATIONS OF LARGE ANIMALS AND ITS IMPLICATIONS FOR CRYPTOZOOLOGY

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ABSTRACT: Species populations normally have considerable capacity to resist threats to their survival. However, very small populations, and hence, very rare species, have much less capacity to resist those threats because of their increased susceptibility to the deleterious effects of stochastic events. Three stochastic processes play extremely important roles in the survival of small populations; these are (1) environmental uncertainty, (2) populational uncertainty, and (3) genetic uncertainty.

A population consisting of fewer than 20 breeding individuals is at serious risk of extinction from the effects of all three types of uncertainty. This fact alone suggests that small populations of large animals, as typically reported in the cryptozoology literature, are not very likely to have persisted from some time in the distant past, at least at their projected present population sizes. If such populations do exist at the present time, they are precipitously close to extinction.

INTRODUCTION

The primary premise of cryptozoology is that undiscovered populations of known animals may exist in unexpected places (e.g., the mountain lion, *Felis concolor,* in the eastern United States), and that undiscovered species may exist in poorly explored or otherwise inaccessible localities (e.g., the "monsters" in Loch Ness). Thus, animals of interest to cryptozoology have populations that are either supposed to be sparsely distributed over a large area, or exist as a small group in one particular spot; both cases involve small numbers of animals. The question I will address here is whether populations of such animals are likely to exist in a viable state.

Population biologists have only recently become interested in the problem of population viability, primarily as a response to the increasing threats of extinction for dozens of endangered species. As one example, the requirement to manage National Forest System habitats to maintain "viable populations of wildlife and fish" (Salwasser, Mealey, and Johnson 1984) led to a series of workshops sponsored by the U.S. Forest Service to explore the concept of minimum viable population size. These workshops stimulated considerable theoretical work on this problem, and a book will soon be published on this topic (Soulé 1987).

The most important theoretical conclusion from work in this area is that stochastic processes play an extremely critical role in the survival of small populations. These processes separate naturally into three categories: (1) environmental uncertainty, (2) populational uncertainty, and (3) genetic uncertainty. Uncertain environmental factors range from major catastrophes (e.g., fires, earthquakes, major storms, pandemic disease, etc.) to mildly unpredictable environmental variation, such as year-to-year changes in weather patterns. Uncertain demographic factors include random variations in sex ratio, age of first reproduction, number of offspring, distribution of offspring over the lifetime of an individual, and time of death. Genetic uncertainty includes inbreeding (the mating of related individuals), and loss of variation through genetic drift.

POPULATION VIABILITY IN GENERAL

In the most general terms, a population's short- and mid-term survival potential is determined primarily by its resilience and its fitness. Resilience refers to a population's ability to survive in the face of normal birth and death events, which in turn are determined by the species' reproductive potential, social system, generation time, and the nature and severity of random environmental perturbations. A population's fitness depends on its having the appropriate set of genes to cope with its environment; this, in turn, is largely determined by the presence of sufficient genetic variation to maintain normal fecundity and viability under the prevailing ecological circumstances. Beyond this, a population's long-term survival potential is related to its adaptability, or its ability to evolve. Adaptability depends upon the maintenance of sufficient genetic variation to adjust to environmental change through the process of natural selection.

Species populations normally have considerable capacity to resist threats to their survival through various kinds of responses, i.e., they have adequate resilience, fitness, and adaptability. However, very small populations, and hence, very rare species, have much less capacity to resist those threats because of their increased susceptibility to the deleterious effects of stochastic events.

DEMOGRAPHIC FACTORS

Demographers usually model population growth by variations of two basic equations. The first is exponential growth:

$$dN/dt = rN$$

where N is the number of individuals in the population and r is the instantaneous rate of increase. It is a fair estimator of population increase in an unlimited environment. Many insect populations, especially those of crop pests, grow exponentially for a time. Eventually, however, something puts the brakes on population growth, and numbers decline, usually precipitously. It is highly unlikely that the exponential growth model has any applicability to cryptozoology.

The second model of population growth is referred to as the logistic equation. Under this model, a population grows exponentially until it reaches a point where the rate of growth begins to decline as resources become increasingly limiting. Eventually, the population stabilizes at a point called the carrying capacity (K), defined as the number of individuals that a given area can support:

$$dN/dt = rN\left(\frac{K - N}{K}\right)$$

This logistic model is more applicable to cryptozoological situations; however, it is generally unrealistic, since few populations have been observed to rise to some level and then remain constant over time. Rather, they fluctuate because the values of r and K change, both deterministically and stochastically.

Fluctuations in r are at the heart of the population persistence problem. Any factor contributing to a decrease in its growth rate is a potential threat to a population's persistence; however, most natural populations continually face such changes without going extinct. This is because some of these factors may be density-dependent. That is, they operate less intensively as population size decreases; or the operation of some negative factors may be discontinuous in time or space, so that they either diminish before exterminating a population, or affect only a segment of it at a time. Thus, most fluctuations in r usually have little long-term effect on the size and persistence probabilities of large populations.

However, as populations become smaller, the risk of extinction increases dramatically. MacArthur (1972) modeled the extinction process as a function of r, K, and the per capita birth rate (b), and predicted that populations with high growth rates, high per capita birth rates, and large K's (in the thousands) had expected times to extinction which were very large. However, for populations with lower r's and b's, extinction was likely to be fairly rapid below a threshold value of K that was in the tens to low hundreds, depending on the values of the former parameters. Since MacArthur's model did not consider the effects of age structure on the population, we have to interpret these figures as the numbers of *breeding individuals,* not total population size. A second model by Richter-Dyn and Goel (1972) also predicted a threshold effect for population persistence of approximately the same order of magnitude. Since large animals tend to have low r's and low b's, these models suggest that large, rare species can persist if the number of breeding individuals in their populations are above these threshhold values.

However, these models do not account for any variability in growth rates that might result from random variation in birth and death processes. May (1973) incorporated these factors, which we now call individual demographic stochasticity or Vi, into a second-generation model, and concluded that

random fluctuations in population size should be roughly proportional to $1/\sqrt{K}$. This implies that Vi will result in a population of about 100 individuals varying between 90 and 110 ($100 \pm \sqrt{K}$, or 10). Thus, May's result suggests that the effects of individual demographic stochasticity are unlikely to cause extinction in any but the smallest populations.

More recent models by Leigh (1981) and Goodman (1987) tend to support this conclusion. These models show that Vi is an important factor only for the survival of very small populations, and the importance of Vi declines rapidly with increases in population size. This is because individual variations in survivorship or reproduction tend to be compensated by the contributions of more and more individuals. Thus, as populations achieve even relatively modest numbers, predicted times to extinction calculated on the basis of Vi alone become quite large.

However, these models also make a critical point: the expected survival time of a population depends critically on the variability of its growth rate, and this variability actually consists of *two* components, the individual demographic stochasticity (Vi) modeled above, and environmental stochasticity (Ve). This second component, environmental stochasticity, is essentially independent of population size, and it poses problems for population persistence that can be extremely severe. Examples of this kind of variation are population-wide changes in the probabilities of death or reproduction related to the vagaries of climate, disease, competition, predation, or resource availability. Goodman's model shows that, with realistic estimates of the effects of Ve factored in, times to extinction become much shorter and much less responsive to higher values of K than those predicted by previous models which only considered the effects of Vi. Furthermore, environmental stochasticity results in times to extinction which increase only gradually with population size, rather than exhibiting threshold effects. If environmental variability is high, very large K's are required to achieve reasonably long times to extinction. Even an increasing population can have a relatively short predicted time to extinction if it has a low rate of increase and a relatively high variance in this rate.

Taking these factors into consideration, how likely is it that some of the subjects of cryptozoological interest exist as viable populations? Let us look at one example. Sheldon and Kerr (1972) and Scheider and Wallis (1973) calculated the maximum probable population density of monsters in Loch Ness based on ecologically defensible principles. Both groups concluded that the lake could support 10–20 individual monsters of 1,000–1,500 kg, and about 8 m long. Larger numbers of smaller animals could be supported, but these would not be suitably monstrous. Even if we assume that 20 monsters could live in the lake, it is extremely unlikely that all of them would be members of the breeding population; some are likely to be too old, and others too young to reproduce.

A population consisting of fewer than 20 breeding individuals is at serious risk of extinction from the effects of individual demographic stochasticity alone, and a population of this size could not withstand the effects of any environmental stochasticity whatsoever. Although Loch Ness has a fairly constant temperature of about 5.6°C. (Rines *et al.* 1976), other factors, such as food supply, are probably much more important potential contributors to a disastrous population-wide fluctuation in birth or death probabilities. Thus, we can conclude that the persistence of a viable population of monsters in Loch Ness from some indefinite time in the past is extremely unlikely. Even if 20 individuals do exist there at the moment, the population is precipitously close to extinction.

Genetic Factors

In addition to random demographic factors, genetic uncertainty can threaten population viability as well. Genetic uncertainty refers to random changes in a population's genetic makeup which have deleterious effects on the ability of individuals to survive and reproduce, as well as on the capacity of populations to respond adaptively to changes in their environments. The two major genetic factors causing deleterious effects are inbreeding depression and genetic drift.

Inbreeding depression results from the expression of deleterious genes as a result of the mating of close relatives. Most populations carry a "genetic load" of deleterious alleles. These alleles are usually rare and not particularly harmful in the heterozygous state; however, when closely related individuals mate, the chance of their offspring inheriting deleterious alleles in the homozygous state is increased. When deleterious alleles appear as homozygotes, they often result in the decline of various fitness traits such as fertility, fecundity, and viability. If population size is large enough, natural selection can eliminate the individuals expressing the deleterious recessive alleles, and the effects on the population as a whole will be minimal. However, if the population size is too small for selection to work effectively, the deleterious genes may become fixed in the population.

Furthermore, the deleterious effects of inbreeding can interact with random demographic events and result in even more severe threats to the persistence of small populations. For example, as population size becomes smaller, the incidence of inbreeding is likely to increase. As inbreeding increases, the incidence of reproductive failure is likely to increase as well. This results in a further reduction of population size, increasing inbreeding even more. Soon, a population can be caught in a downward spiral of ever decreasing viability, generally leading to its extinction.

Random changes in gene frequencies in populations are called genetic drift; these random changes sooner or later result in the loss of genetic variation, the rate of loss being dependent on population size. In small

populations, this loss can be quite severe and rapid. For example, in a population with 10 individuals contributing progeny to subsequent generations, 40% of the genetic variability in the population will be lost within ten generations. As was mentioned earlier, the fitness of a population depends on the presence of sufficient variation in its gene pool to maintain normal fecundity and viability. Likewise, a population's adaptability, or its ability to evolve, also depends on a sufficient reserve of different genes to adjust to environmental change through the process of natural selection.

Thus, in order to maintain population fitness and adaptability, a population must be large enough to prevent intense inbreeding and serious reductions in genetic variation by random drift. Unfortunately, the number of individuals actually involved in contributing progeny—and therefore genes—to subsequent generations is generally only a small fraction of the total population size. A population containing several hundred individuals (N) may have a genetically effective size (Ne) of only 10 or 20 in some species.

The genetically effective size of a population is reduced by any of a variety of factors that represent departures from a genetically ideal situation (Wright 1931). These include the presence of nonbreeding individuals, skewed sex ratios, non-random tendencies for inbreeding or outcrossing, random variation in progeny survivorship, the loss of genetic variability that may have occurred during previous periods of low population size (the "bottleneck" effect), and the tendency of individuals in some species to mate with individuals from an area that may be smaller than the area occupied by the population as a whole (the population structure effect). The cumulative effects of these factors are multiplicative, and are usually expressed as the ratio of Ne/N.

The results of low Ne's on population fitness can be devastating. For example, let us assume that our population of monsters in Loch Ness consists of 20 individuals, and that the ratio of Ne/N is somewhere between 0.2 to 0.4, figures typical of large vertebrates. This means that the genetically effective size of the population is between 4 and 8. At this size, the expected rate of increase in inbreeding in each generation (ΔF) is equal to 1/[2Ne], or between 6 and 13%. This is well above the level where natural selection for performance and fertility can balance inbreeding depression, which is about 1% (Frankel and Soulé 1981).

The loss of heterozygosity in this population can be estimated by the formula

$$H = (1 - 1/2N)^t$$

where t is the number of generations involved. With Ne's this small, about 6 to 13% of the genetic variation in the population will be lost each generation. After 10 generations, if Ne's stay the same, only 28–54% of the original

variation will be retained. Losses such as these pose serious threats for short-term survival; survival over longer periods depends on an even broader array of genetic resources.

Summary and Conclusions

According to current theory in population biology, the risk of extinction of a population depends on the number of individuals the habitat can support (K), its per capita birth rate, its rate of growth (r), the variability of its growth rate (Vi and Ve), and its genetically effective size (Ne). Although all populations are at some risk of extinction from various events that affect their demographic patterns and genetic composition, the risk is decidedly greater in small, isolated populations. If a rare species can maintain a minimum breeding population size somewhere above the mid tens to low hundreds, the exact number depending on its growth rate and per capita birth rate, the odds favor its persistence, provided that there is no evironmentally-caused variation in these rates. However, if environmental variation affects birth and death processes in any significant way, a minimum viable population needs to be much larger to avoid extinction from demographic factors alone.

Even at population sizes that are adequate to buffer populations from extinction from the effects of Vi and Ve, low genetically effective sizes can cause additional problems. Ne's below 50 or so result in levels of inbreeding and loss of genetic variation that also threaten short-term persistence. An Ne of 500 is probably the minimum necessary for continuing evolution (Franklin 1980, Frankel and Soulé 1981, Lande 1987). Since the actual number of individuals necessary to maintain an effective population size this large is likely to be considerably greater than 500, it is clear that extreme rarity is a condition that precludes much potential for evolutionary change.

There are a few documented cases of small populations which have persisted for thousands of years. One of the most striking examples is the Devil's Hole pupfish, *Cyprinodon diabolis,* which has survived in a tiny spring in the Nevada desert for 10–20,000 years (Miller 1981) with population sizes fluctuating seasonally from 150 to 400 individuals (Deacon 1979). This rather remarkable situation has resulted at least in part from the physical conditions in this spring, which are very constant, at least until recently, when it has been adversely affected by human activities (Williams *et al.* 1986). The historical influence of Ve on the persistence of this population must have been very small indeed. As predicted, *C. diabolis* has evidently lost all measurable genetic variability (Turner 1974).

Whatever combination of factors may have occurred to allow the Devil's Hole pupfish to hang on in its tiny habitat for tens of millenia, current theory in population biology suggests that its case is a very rare exception. If viable populations of large animals, still unknown to science, are "out there," they must either elude detection very well by sophisticated behavioral traits, or

live in extremely remote or unaccessible areas with virtually constant environments. In either event, they must continue to maintain breeding populations that number in the mid-tens to low hundreds in order to persist.

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